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A new cheirolepidiaceous conifer from the Lower Cretaceous (Albian) of Hokkaido, Japan

KEN'ICHI SAIKI

Department of Plant Science, Natural History Museum and Institute, Chiba 955-2, Aoba, Chuo-ku, Chiba 260-8682, Japan

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Abstract. A new fossil conifer, *Pseudofrenelopsis glabra* sp. nov., (Cheirolepidiaceae) is described based on a single specimen obtained from the Lower Cretaceous Yezo Group (Albian) of Hokkaido, Japan. The new species is characterized by cuticle possessing thin periclinal walls, a well-developed hypodermis, and absence of trichomes on internode and outer leaf surface. Recently, the author described *Frenelopsis pombetsuensis* from the Lower Cretaceous Yezo Group (Albian) of Hokkaido. The family Cheirolepidiaceae is a diagnostic taxon of the Ryoseki-type element that is reported only from the Ryoseki- and the Mixed-type floras. Thus *Pseudofrenelopsis glabra* is the second evidence of the Ryoseki-type element from Hokkaido.

Key words: Albian, conifer, Hokkaido, Middle Yezo Group, *Pseudofrenelopsis glabra*, Ryoseki-type floras.

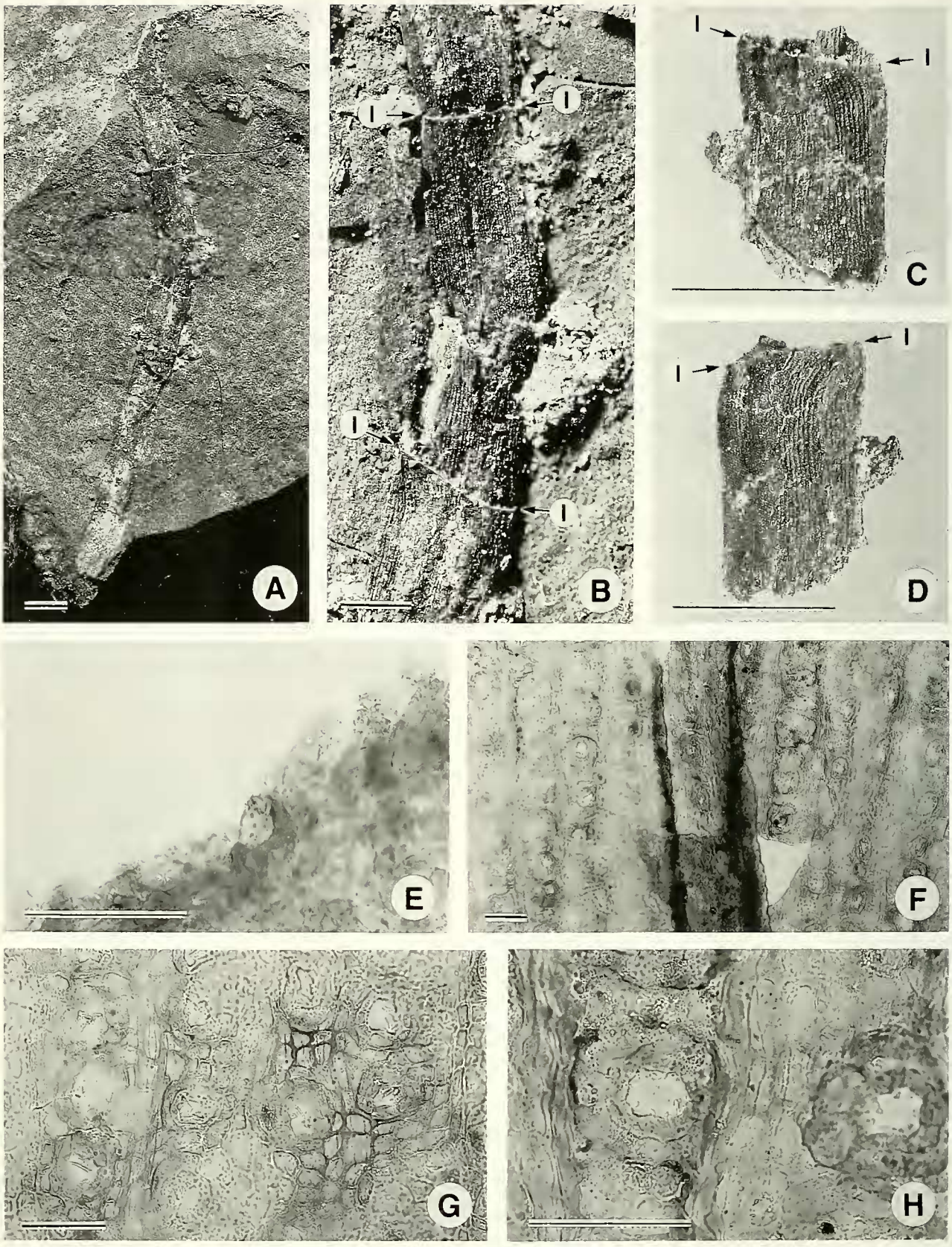
Introduction

Jurassic and Early Cretaceous floras in eastern Eurasia have been classified by Kimura (1980, 1987) and Ohana and Kimura (1995) into three characteristic floras, the Ryoseki- and the Tetori-type floras, and the Mixed-type floras comprising elements of both the Ryoseki- and the Tetori-type floras. According to these authors, the Ryoseki-type floras grew under tropical to subtropical conditions with an annual long arid season, while the Tetori-type floras grew under temperate and moderately humid conditions.

The genus *Pseudofrenelopsis* belongs to the extinct conifer family Cheirolepidiaceae. Although this family is a dominant group of Mesozoic conifers, its closer affinity remain equivocal. The members of the family have various kinds of shoot morphology ranging from *Brachyphyllum-Pagiophyllum*-type shoots bearing scale leaves to *Frenelopsis-Pseudofrenelopsis*-type cylindrical segmented shoots bearing minute leaves. The single most reliable character of this family is possession of the pollen of the genus *Classopollis* Pflug (Watson, 1988). Although the plants yielding fossil remains attributed to the genus *Pseudofrenelopsis* were widely distributed during the Early Cretaceous (Berriasian-Albian) of North America, Europe, North Africa and Asia, they were apparently restricted to the Cretaceous (Table 1).

The frenelopsids, which include the genus *Pseudofrenelopsis* and the closely related genus *Frenelopsis*, have been used as indicator taxa of tropical to subtropical arid climate (Alvin, 1982). In east Asia the occurrence of the frenelopsids in fossil floras is restricted to the Ryoseki- and the Mixed-type floras. Although *Frenelopsis* is known from the Ryoseki-type floras of the Upper Jurassic to Lower Cretaceous in Japan, fossil remains assigned to *Pseudofrenelopsis* have not been reported yet. In the present paper, the remains of shoot and associated cuticular features of *Pseudofrenelopsis* from Japan are described.

Figure 1. Map of Hokkaido, Japan showing the location of the Pombetsu Valley.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Material and Methods

Material.—A compressed conifer shoot was found in the Pombetsu Valley about 60 km northeast of Sapporo (Figure 1). The specimen was obtained from the mudstone bed of the so-called "Main part of Middle Yezo Group". The locality is situated between Matsumoto's outcrops Ik 2025 and 2031, from where the Albian ammonite *Ammonoceratites yezoensis* Yabe has been reported (Matsumoto, 1965, fig. 3).

Methods.—Fossil remains were immersed in Schulze's solution followed by diluted NaOH. The cuticle was mounted in Eukitt for light microscopy. For SEM observation, cuticles were coated with Pt-Pd in a Hitachi E-1030 ion sputter and photographed with Hitachi S-800.

All specimens used in this study are deposited in the Mikasa City Museum (MCM), Ikushumbets-nishikicho, Mikasa, Hokkaido.

Systematic description

Order Coniferales
Family Cheirolepidiaceae Takhtajan, 1963
Genus ***Pseudofrenelopsis*** Nathorst, 1893

Remarks of the genus.—The diagnosis originally based only on the type species was emended by Watson (1977) after studying specimens of *Frenelopsis varians* Fontaine, which is now placed in this genus. Recently, Srinivasan (1995) emended the diagnosis of *Pseudofrenelopsis* based on new morphological characters of Puddledock material. Srinivasan's concept is followed here.

Pseudofrenelopsis glabra sp. nov.

Figures 2A-H, 3A-I

Material.—Holotype, MCM-P030

Horizon.—Main part of the Middle Yezo Group (Albian).

Type locality.—Pombetsu Valley, Mikasa, Hokkaido (Figure 1; ca. 43°16′31″N, 141°59′20″E). The locality is about 80 m south of Matsumoto's (1965) outcrop Ik 2031.

Diagnosis.—Segmented shoot bears a simple spiral of leaves, each leaf encircling the stem. Leaf margin having hairs; outer surface of both abaxial and adaxial leaf cuticle smooth, without trichomes. Internode cuticle well developed. Outer surface of cuticle smooth, nonpapillate. Stomata arranged in longitudinal rows. Stomatal complex consisting of a pair of guard cells and 7-9 subsidiary cells. Guard cells sunken below a ring of subsidiary cells with irregularly oriented apertures. Stomatal pit rounded in surface view. Outer surface of subsidiary cells forming a raised rim bounded by a deep groove around stomatal pit. A well-developed cutinized hypodermis of thin-walled cells covering most of the internal surface of the cuticle.

Description.—A single compressed shoot was obtained (Figures 2A, B). The shoot is segmented, bearing a simple spiral of leaves. Each of the leaves encircles the stem. The internode is 6-9 mm long and 4 mm wide (Figures 2A, B). Triangular part of the leaf is up to 1.5 mm high at a node (Figures 2B, C; 3A). The leaf margin has hairs up to 40 μm long (Figures 2E; 3B, C). Outer surface of both abaxial and adaxial leaf cuticle is smooth, without trichomes (Figures 3B-D).

The internode cuticle is well developed, about 8 μm in total thickness. The cuticle consists of outer periclinal epidermal wall about 3 μm thick, anticlinal wall and thinly cutinized hypodermis (Figure 3E). No dorsiventrality is observed (Figure 2F). Stomata are about the same optical density as the rest of cuticle and are arranged in well marked longitudinal rows in 7-9 rows per mm. Each row of stomata is a single stoma wide. 70-100 per mm^2 in density. (Figures 2F, G; 3F, G). The bands of epidermal cells between the rows of stomata are 20-70 μm (1-3 cells) wide, consist of longitudinally arranged epidermal cells. The epidermal cells are elongated rectangular to polygonal in shape, 25-50 μm long and 10-25 μm wide (Figures 2F, G; 3G). Outer surface of the cuticle is smooth, nonpapillate (Figure 3F).

The stomatal complex is 80-120 μm in diameter, consists of a pair of guard cells and 7-9 subsidiary cells (Figure 3G). The guard cells are 40-70 μm long and 10 μm wide and are sunken below a ring of subsidiary cells. The aperture of the stoma is irregularly oriented (Figure 3G). The stomatal pit is about 30 μm in diameter and is rounded in surface view (Figures 3F, H). Outer surface of the subsidiary cells forms a raised rim bounded by a deep groove around stomatal pit. Each of the subsidiary cells has a single papilla projecting into the stomatal pit (Figures 2H; 3F, H, I).

A well developed cutinized hypodermis of thin-walled cells cover most of the internal surface of the cuticle except for the region immediately beneath each stomatal apparatus. The hypodermal cells are rectangular or polygonal under the stomatal zone and are axially elongate rectangular under the nonstomatal zone (Figures 3E, G).

Discussion.—Due to the fragmentary nature of the fossil specimen the arrangement of the branch system of *Pseudofrenelopsis glabra* is uncertain. External and cuticular observations of the specimen clearly indicate the absence of a groove or suture separating the basal cushions, as seen in living species of the Cupressaceae.

Although the epidermal cells are clearly visible with light microscopy (Figure 2G), SEM microscopy of the inner surface of cuticle shows only hypodermis and stomatal complexes,

Figure 2. *Pseudofrenelopsis glabra* sp. nov. (MCM-P030). **A**: Holotype (MCM-P030). **B**: Middle region of the holotype showing leaf margins (l). **C, D**: Opposite sides of the same shoot fragment showing the margin of a single leaf (l). **E**: Light microscope image of the leaf margin showing short hairs. **F**: Light microscope image of cuticle from internodal region showing fold represented by central dark line, and cuticles of both sides of the compressed specimen. Arrangement of stomata and epidermal cells show no siginificant difference on both sides of the cuticles. **G**: Light microscope image of cuticle from the internodal region showing longitudinally arranged stomata, light microscope. **H**: Light microscope image of stomata, focused through the stomatal pit showing the papillae. Scale bars = 5 mm in A-D; 100 μm in E-H.

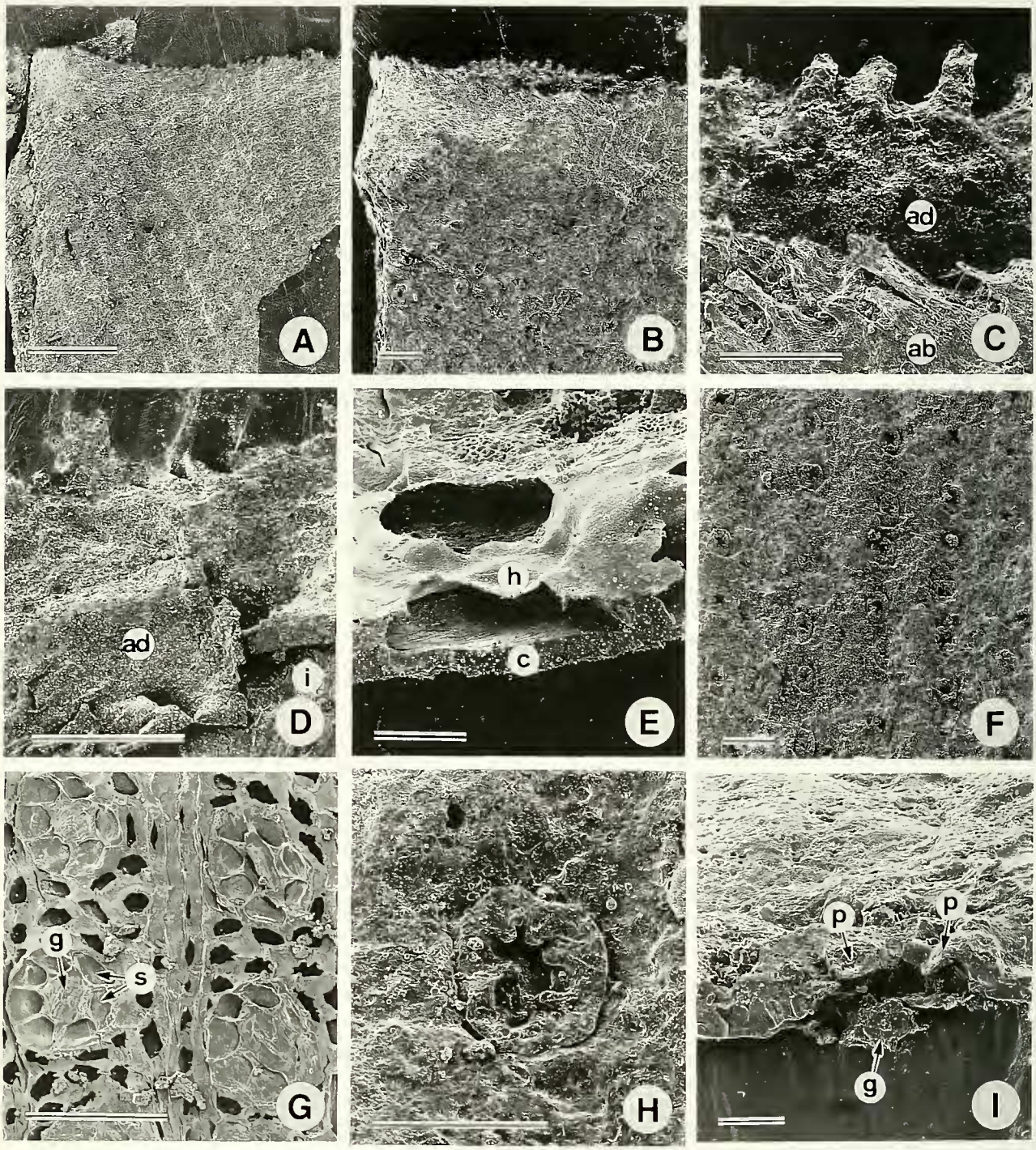

Figure 3. SEM micrographs of *Pseudofrenelopsis glabra* sp. nov. cuticle (MCM-P030). **A**: Triangular free part of leaf. **B**: Edge of a leaf, showing marginal hairs and outer surface of abaxial leaf cuticle. **C**: Enlarged photo of 3B showing the short marginal hairs and smooth outer surface of the abaxial (ab) and adaxial (ad) leaf cuticle. **D**: Surface view of adaxial leaf cuticle (ad) and inner view of cuticle from the internodal region (i). **E**: Section of cuticle showing cutinized epidermis (c) and hypodermis (h). **F**: Outer view of cuticle from the internodal region showing mouth of stomatal pit. **G**: Cuticle from the internodal region showing longitudinally arranged stomatal complexes. Inner view of stomatal complexes showing the guard cells (g), and subsidiary cells (s). **H**: Outer view of a stoma showing the rounded mouth of the stomatal pit with papillae. **I**: Section of stoma showing guard cells (g), and papillae in throat of stoma (p). Scale bars=500 μm in A, B; 50 μm in C, D, F-H; 10 μm in E, I.

Table 1 Comparative morphometices of *Pseudofrenelopsis glabra* sp. nov. and related species.

Characters/Species	***P. varians***	***P. parceramosa***	***P. papillosa***	***P. dalatzensis***	***P. heishanensis***	***P. nathorstiana***	***P. glabra*** sp. nov.
Internode length	1.5–17 mm	1–11 mm	5–11 mm	5.5–10 mm	5–6 mm	1.0–2.9 mm	6–8 mm
Internode width	3–7 mm	1 mm<	3–7.5 mm	3–6.5 mm	2.5–4 mm	1.0–2.0 mm	4 mm
Presence of suture or gap	none	in some 'open' form	none	none	none	yes	none
Maximum length of free leaf	1.5 mm	2 mm	1.5 mm	2 mm	2 mm	1.0 mm	1.5 mm
Leaf margin	hairs up to 60 μm	hairs up to 80 μm	hairs up to 80 μm	without hairs	without hairs	hairs up to 145.0 μm	hairs up to 40 μm
Trichomes or hairs on adaxial surface of leaf	hairs present	hairs present	hairs present	normally without hairs	without hairs	trichomes	without hairs
Internode cuticle thickness	50–110 μm	30 μm	5–7.5 μm	(5–)7.5–10(–25)μm	3–5 μm	10.0 μm	3 μm
Trichomes or hairs on epidermal cells	up to 80 μm	none to very long hairs	usually present	with large papillae	none	up to 200 μm	none
Cutinized hypodermis	in "open" leaf-base cushions	well cutinized	none	none	none	none	well cutinized
Stomatal arrangement	scatterred in "closed" form, rows in "open" form	well defined rows	longitudinal rows with scattered stomata	well defined rows	well defined rows	mostly ill defined rows	well defined rows
Density of stomatal rows	8–10 per mm	6–10 per mm	(4–)6–7(–9) per mm	(6–)7–8(–10) per mm	8–9(–10) per mm	11–12 per mm	7–9 per mm
Diameter of stomatal apparatus	70–100 μm	50–80 μm	40–92.5 μm	55–95 μm	62.5–100 μm	50–73×54–62 μm rarely 103.0 μm	80–120 μm
Number of subsidiary cells	(4–)5–8(–9)	(4–)5–6(–7)	(4–)5–6(–8)	5–6	5–6(–7)	(4–)5–6(–7)	6–8
Rim of stomatal pit	round: –with papillae	round: –with or without papillae	round: –with papillae	stellate	stellate	elliptical to round: –with papillae	round: –with papillae
Stratigraphic range	Aptian–Albian	Berriasian–Albian	Lower Cretaceous	Lower Cretaceous	Aptian–Albian	lower–mid-Albian	Albian
Distribution	North America	North America, Europe	China	China	China	China	Japan
References	Watson, 1977	Alvin, 1977 Alvin *et al*. 1978 Watson, 1977	Chow and Tsao, 1977 Zhou and Cao, 1979 Zhou, 1995	Chow and Tsao, 1977 Zhou, 1995	Zhou, 1995	Srinivasan, 1995	

because the epidermal cells are covered by cutinized hypodermis (Figure 3G).

Comparison.—Although the present specimen is fragmentary, both external and cuticular features of the specimen correspond well with the diagnosis of *Pseudofrenelopsis* Nathorst emended by Srinivasan (1995) in its segmented shoot bearing a simple spiral of leaves, smooth cylindrical internode, and guard cells sunken below ring of subsidiary cells.

Among the species of *Pseudofrenelopsis* previously described, the European *P. varians* (Fontaine) Watson and American *P. parceramosa* (Fontaine) Watson differ from *P. glabra* in possessing an extremely thick cuticle and having trichomes on the adaxial surface of the leaf cuticle (Watson, 1977).

Although various species of *Pseudofrenelopsis* have been reported from China, most are provided with brief descriptions (Zhou, 1995). Recently, Zhou (1995) reexamined and combined the Chinese *Pseudofrenelopsis* into the following three species : *P. papillosa* (Chow et Tsao) Zhou, *P. dalatzensis* (Chow et Tsao) Zhou, and *P. heishanensis* Zhou (Table 1). *Pseudofrenelopsis glabra* is similar to these Chinese species in possessing a thinner internode cuticle than the European and American species. *Pseudofrenelopsis dalatzensis* and *P. heishanensis* can be distinguished from *P. glabra* by the stellate rim of the stomatal pit and absence of hairs on their leaf margins.

The shape of the cells, smooth periclinal walls, and thin anticlinal walls of the hypodermis of *Pseudofrenelopsis glabra* (Figures 3G, E) are very similar to the "epidermal cells" of *Pseudofrenelopsis heishanensis* described by Zhou (1995). However, detailed light and SEM microscopy of *P. heishanensis* is required prior to meaningful comparison of *P. heishanensis* and *P. glabra*.

Pseudofrenelopsis papillosa, redescribed in detail by Zhou (1995), possesses the most similar cuticle to that of *P. glabra* in having hairs on the margin of the leaf, round stomatal pits, and a thin cuticle. These resemblances may indicate a close phylogenetic relationship between these two species. *Pseudofrenelopsis glabra* is however, clearly distinguished from *P. papillosa* by a smaller number of subsidiary cells and absence of trichomes on the outer surface of the leaf adaxial cuticle.

Paleophytogeography.—Since Kimura (1961, 1975) has divided the Late Jurassic-Early Cretaceous floras of Japan and its adjacent areas into the Ryoseki-type and the Tetori-type floras, this paleophytogeographical distinction has been extended to East Asia with some modification, and the Mixed-type flora that consist predominantly of the Ryoseki-type element and subordinate Tetori-type element was added (Kimura, 1980, 1987 ; Kimura and Ohana, 1992 ; Cao, 1994 ; Ohana and Kimura, 1995).

Although the Mesozoic flora of Hokkaido is famous for its well preserved permineralized materials, the stratigraphic range of these materials is restricted to the Upper Cretaceous (Nishida, 1991). So far, the absence of Jurassic and Lower Cretaceous fossil plants from Hokkaido had prevented comparison of the Early Cretaceous flora of Hokkaido with the Ryoseki- and the Tetori-type floras. Recently, Saiki (1997) described *Frenelopsis pombetsuensis*, from the Lower Cretaceous Yezo Group (Albian) of Hokkaido. The family Cheirolepidiaceae is a diagnostic taxon of the Ryoseki-type element reported only from the Ryoseki- and the Mixed-type floras (Ohana and Kimura, 1995). Thus, *Pseudofrenelopsis glabra* is the second evidence of the presence of Ryoseki-type element from Hokkaido.

Ohana and Kimura (1995) estimated that the Ryoseki-type floras flourished under tropical or subtropical conditions with an annual long arid season. Their idea is consistent with the thermophilous nature of frenelopsids proposed by Alvin (1982) based on the distribution of frenelopsids of the world and their possession of a thick cuticle. However, the two frenelopsids species from Hokkaido lack two of the xeromorphic features observed in many other frenelopsids, namely, a thick cuticle and trichomes on the internode surface. The cuticle thickness of eight species listed in Alvin (1982) are 8-110 μm thick in their periclinal wall rather than 3 μm and 3-4 μm thick as in *Frenelopsis pombetsuensis* and *Pseudofrenelopsis glabra* respectively. The cuticular features of *Frenelopsis pombetsuensis* and *Pseudofrenelopsis glabra* may reflect the rather humid condition inferred for the Albian of Pombetsu, rather than the xeric conditions from other regions of the world where frenelopsids were distributed (Alvin, 1982). This assumption is consistent with recent palynological data indicating that the group inhabited a variety of ecological niches (Watson, 1988).

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References cited

Alvin, K.L., 1977 : The conifer *Frenelopsis* and *Manica* in the Cretaceous of Portugal. *Palaeontology*, vol. 20, p. 387-404.

Alvin, K.L., 1982 : Cheirolepidiaceae : Biology, structure and paleoecology, *Review of Palaeobotany and Palynology*, vol. 37, p. 71-98.

Alvin, K.L., Spicer, R.A. and Watson, J., 1978 : A *Classopollis*-containing male cone associated with *Pseudofrenelopsis*. *Palaeontology*, vol. 21, p. 847-856.

Cao, Z., 1994 : Early Cretaceous floras in Circum-Pacific region of China. *Cretaceous Research*, vol. 15, p. 317-332.

Chow, T.Y. and Tsao, C.Y. 1977 : On eight new species of conifers from the Cretaceous of East China with reference to their taxonomic positiion and phylogenetic relationship. *Acta Palaeontologica Sinica*, vol. 16, no. 2, p. 165-181. (*in Chinese with English summary*)

Kimura, T., 1961 : Mesozoic plants from the Itoshiro Sub-

group, the Tetori Group, Central Honshu, Japan. part 2. *Transactions and Proceedings of the Palaeontological Society of Japan, New Series*, no. 41, p. 21-32.

Kimura, T., 1975 : Notes on the Early Cretaceous floras of Japan. *Bulletin of the Tokyo Gakugei University, Series 4*, vol. 27, p. 217-257.

Kimura, T., 1980 : The present status of the Mesozoic land floras of Japan. *Professor Saburo Kanno Memorial Volume*, p. 379-413. Tsukuba University.

Kimura, T., 1987 : Geographical distribution of Palaeozoic and Mesozoic plants in East and Southeast Asia. *In*, Taira, A. and Tashiro, M. *eds.*, *Historical Biogeography and Plate Tectonic Evolution of Japan and Eastern Asia*, p. 135-200. Terrapub, Tokyo.

Kimura, T. and Ohana, T., 1992 : Cretaceous palaeobotany and phytogeography in Eastern Eurasia. *Palaeontological Society of Korea, Special Publication*, no. 1, p. 27-34.

Matsumoto, T., 1965 : A monograph of the Collignoniceratidae from Hokkaido, part 1. *Memoirs of the Faculty of Science, Kyushu University, Series D*, no. 16, p. 1-80.

Nishida, H., 1991 : Diversity and significance of Late Cretaceous permineralized plant remains from Hokkaido, Japan. *Botanical Magazine Tokyo*, vol. 104, p. 253-273.

Ohana, T. and Kimura, T., 1995 : Late Mesozoic phytogeography in eastern Eurasia, with special reference to the origin of angiosperms in time and site. *Proceedings of 15th International Symposium of Kyungpook National University*, p. 293-328.

Saiki, K., 1997 : *Frenelopsis pombetsuensis* : a new cheirolepidiaceous conifer from the Lower Cretaceous (Albian) of Hokkaido, Japan. *Paleontological Research*, vol. 1, no. 2, p. 126-131.

Srinivasan, V., 1995 : Conifers from the Puddledock locality (Potomac Group, Early Cretaceous) in eastern North America. *Review of Palaeobotany and Palynology*, vol. 89, p. 257-286.

Watson, J., 1977 : Some lower Cretaceous conifers of the Cheirolepidiaceae from the U.S.A. and England. *Palaeontology*, vol. 19, p. 715-749.

Watson, J., 1988 : The Cheirolepidiaceae. *In*, Beck, C.B. *ed.*, *Origin and Evolution of Gymnosperms*, p. 382-447. Columbia University Press, New York.

Zhou, Z., 1995 : On some Cretaceous pseudofrenelopsids with a brief review of cheirolepidiaceous conifers in China. *Review of Palaeobotany and Palynology*, vol. 84, p. 419-438.

Zhou, Z. and Cao, Z., 1979 : Some Cretaceous conifers from southern China and their stratigraphical significances. *In*, Institute of Vertebrate Palaeontology and Palaeoanthropology, and Nanjing Institute of Geology and Palaeontology, Academia Sinica *eds*, *Mesozoic and Cenozoic Red Beds of Southern China*, p. 218-222. Science Press, Beijing.

Ikushumbets-nishikicho 幾春別錦町, Mikasa 三笠, Pombetsu 奔別